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Abstract

The impact of environmental variability on population size growth rate in dynamic models is a recurrent issue in the theoretical ecology literature. In the scalar case, R. Lande pointed out that results are ambiguous depending on whether the noise is added at arithmetic or logarithmic scale, while the matrix case has been investigated by S. Tuljapurkar. Our contribution consists first in introducing another notion of variability than the widely used variance or coefficient of variation, namely the so-called convex orders. Second, in population dynamics matrix models, we focus on how matrix components depend functionaly on uncertain environmental factors. In the log-convex case, we show that, in a sense, environmental variability increases both mean population size and mean log-population size and makes them more variable. Our main result is that specific analytical dependence coupled with appropriate notion of variability lead to wide generic results, valid for all times and not only asymptotically, and requiring no assumptions of stationarity, of normality, of independency, etc. Though the approach is different, our conclusions are consistent with previous results in the literature. However, they make it clear that the analytical dependence on environmental factors cannot be overlooked when trying to tackle the influence of variability.

Key words: environmental variability; matrix population models; growth rate; stochastic orders; log-convex functions.

Contents

1 Influence of environmental noise on population size

We recall here different observations and results in the theoretical ecology literature which point out the ambiguous role of environmental noise on population size in matrix population models, according to whether the noise is added at arithmetic or logarithmic scale.

1.1 Lande's comments on additive noise at arithmetic or logarithmic scale

R. Lande in [1] comments the influence of environmental noise on population size according to whether the noise is added at arithmetic or logarithmic scale. The evolution of population size $N(t)$ in absence of density-dependent effect may be described

- either on arithmetic scale with multiplicative growth rate $\lambda(t)$ and dynamic $N(t+1) = \lambda(t)N(t)$,
- or on logarithmic scale with growth rate on the log scale $r(t) = \log\big(\lambda(t)\big)$ and dynamic on the log scale $\log N(t+1) = r(t) + \log N(t)$.

On the one hand, adding environmental noise to multiplicative growth rate as in $\lambda(t) = \overline{\lambda} + \epsilon(t)$, where the noise is zero-mean ($\mathbb{E}[\epsilon(t)] = 0$), gives the following mean of growth rate on the log scale

$$\overline{r} = \mathbb{E}[\log\big(\lambda(t)\big)] \approx \log\overline{\lambda} - \sigma_r^2 \, .$$

"Thus, demographic and environmental stochasticity reduce the mean growth rate of a population on the logarithmic scale, compared with that in the (constant) average environment" [1].

On the other hand, adding environmental noise to growth rate on the log scale as in $r(t) = \overline{r} + \epsilon(t)$ gives, in case $\epsilon(t)$ follows a Normal distribution $\mathcal{N}(\overline{\epsilon}, \sigma_\epsilon^2)$, the following mean of growth rate on the arithmetic scale

$$\overline{\lambda} = \exp\left(\overline{r} + \overline{\epsilon} + \frac{\sigma_\epsilon^2}{2}\right) .$$

Thus, Lande concludes that, "with the mean environmental effect equal to zero, $\overline{\epsilon} = 0$, then it would be found that environmental stochasticity increases the mean multiplicative growth rate, $\overline{\lambda}$".

1.2 Tuljapurkar's asympotic approximation

S. Tuljapurkar considers a stationary sequence of random matrices A_0, A_1, ... yielding population vector $n(t) = A_{t-1} \cdots A_0 n(0)$ and population size $N(t) = \|A_{t-1} \cdots A_0 n(0)\|$. Under general conditions (see [2, 3]), there exists a deterministic *stochastic growth rate* λ_s defined by

$$\log \lambda_s = \lim_{t \to +\infty} \frac{1}{t} \log N(t) = \lim_{t \to +\infty} \frac{1}{t} \log \|A_{t-1} \cdots A_0 n(0)\| .$$

Denoting by λ_1 the largest eigenvalue of the average matrix $\overline{A}$, Tuljapurkar obtains the approximation

$$\log \lambda_s \approx \log \lambda_1 - \frac{\tau^2}{2\lambda_1^2} + \frac{\theta}{\lambda_1^2}$$

where τ^2 is proportional to the variance $\mathbb{E}[(A_t - \overline{A}) \otimes (A_t - \overline{A})]$ (and θ is related to autocorrelation). In this case, environmental stochasticity reduces the mean growth rate of the population.

1.3 A quest for generic results

The two above cases show that environmental noise has an ambiguous impact on population size in matrix population models. Our main objective is contributing to clarify this impact with generic mathematical results. For this, we shall first introduce in Sect. 2 a tool to measure variability, distinct from the widely used variance or coefficient of variation, and known as *convex partial orders*. Then, in Sect. 3, we shall provide generic results on environmental noise variability in population dynamics matrix models. We conclude in Sect. 4 by pointing out proximities and differences between our approach and those presented in Sect. 2.

2 Convex orders as tools for measuring variability

To a (square integrable) random variable X, one can attach the variance $\mathsf{var}(X)$. This latter scalar measures "variability", and any pair of random variables X and Y may be compared, with X being more variable than Y if $\mathsf{var}(X) \geq \mathsf{var}(Y)$. The variance thus defines a *total order*.

Other orders are interesting for comparing pairs of random variables. However, they are generally not total: not all pairs may be ranked. Related to this is the fact that no single scalar, such as variance, may be attached to a random variable to measure its variability. In this vein, we shall present the so-called *increasing convex* and *convex stochastic orders*. Such orders can only rank random variables for which the primitives of their respective repartition functions never cross.

We think that these orders and many others referenced in the two main books [4, 5] may be useful in the ecological modelling scientific community. Of course, for this, practical tests must be developed to compare empirical data as to their variability. This is not the object of this paper.

All random variables are defined on a probability space with probability $\mathbb{P}$. To a random variable X, we shall attach its (right-continuous) *repartition function* $F(x) = \mathbb{P}(X \leq x)$. We shall always consider random variables with finite means, with generic notation X and Y, and F and G for their respective repartition functions.

2.1 Increasing convex order

The increasing convex order compares random variables according both to their "location" and to their "variability" or "spread" [5]. We say that X *is less than* Y *in increasing convex order*, denoted by

$$X \preceq_{icx} Y \ ,$$

if and only if one of the following equivalent conditions holds true

- the primitive of the repartition function of X is always below that of Y: $\int_{-\infty}^{c} F(x)dx \leq \int_{-\infty}^{c} G(x)dx$, for all $c \in \mathbb{R}$,
- $\mathbb{E}(\varphi(X)) \leq \mathbb{E}(\varphi(Y))$ for all increasing and convex function φ.

Roughly speaking, Y is more likely to take on extreme values than X. In a sense, X is both "smaller" and "less variable" than Y [5]. We have the important property that, when $X \preceq_{icx} Y$, the means are ordered too: $\mathbb{E}(X) \leq \mathbb{E}(Y)$. However, nothing can be said of the variances. To compare variances, we need a stronger (more demanding) order.

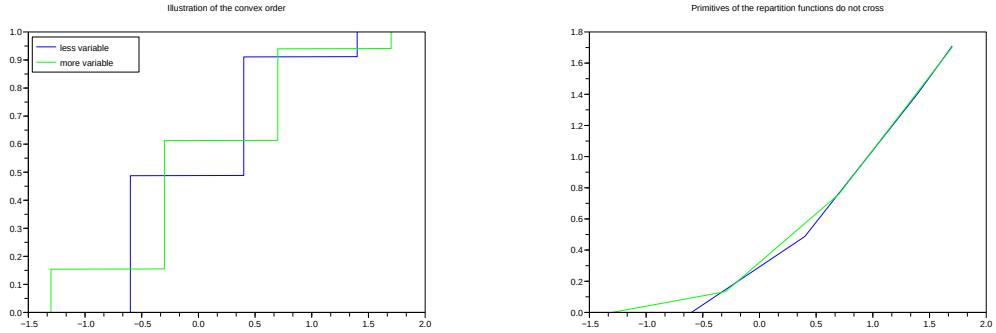
2.2 Convex order

The convex order compares random variables according to their "variability" or "spread" [5]. We say that X *is less than* Y *in convex order*, denoted

$$X \preceq_{cx} Y \ ,$$

if and only if one of the following equivalent conditions holds true:

- the means are equal and the primitive of the repartition function of X is always below that of Y, that is, $\mathbb{E}(X) = \mathbb{E}(Y)$ and $X \preceq_{icx} Y$,



(a) Repartition functions

(b) Primitives

Figure 1: Illustration of the convex order: the primitives of the repartition functions do not cross each other

- $\mathbb{E}(\varphi(X)) \leq \mathbb{E}(\varphi(Y))$ for all convex function φ.

Roughly speaking, Y is more likely to take on extreme values than X (see Figure 1). Notice that the convex order is more demanding than the increasing convex order since the class of "test functions" is larger: all convex functions and not only the increasing convex ones. This is why we obtain stronger important properties that, when $X \preceq_{cx} Y$, the means are equal $\mathbb{E}(X) = \mathbb{E}(Y)$, and the variance are ordered $\mathsf{var}(X) \leq \mathsf{var}(Y)$.

2.3 Some properties

- This *icx* and *cx* orders are stricter than the order defined by comparing variances: not all pairs of random variables may be ranked.

- Consider the class $\mathbb{M}_{\mu,\sigma^2}$ of random variables having same mean μ and variance σ^2. Elements of $\mathbb{M}_{\mu,\sigma^2}$ cannot be compared with respect to *cx*. Indeed, if $X \preceq_{cx} Y$ and $\mathsf{var}(X) = \mathsf{var}(Y)$, then X and Y have the same distribution [4, p.57].

- Adding zero mean independent noise to a random variable increases variability: if Z is independent of X and has zero mean, then X is less than $Y = X + Z$ in convex order. This is a consequence of Strassen's Theorem [4, p.23]. More generally, without assuming independence, X is less than $Y = X + Z$ in convex order whenever the conditional expectation $\mathbb{E}[Z|X] = 0$.

- Consider X following Normal distribution $\mathcal{N}(\mu, \sigma^2)$ and Y following $\mathcal{N}(\nu, \tau^2)$. Then, $X \preceq_{icx} Y$ if and only if $\mu \leq \nu$ and $\sigma^2 \leq \tau^2$, and $X \preceq_{cx} Y$ if and only if $\mu = \nu$ and $\sigma^2 \leq \tau^2$ [4, p.62].

- For $p > 0$, let us introduce $\mathsf{CV}_p(X) := \frac{\mathbb{E}(X^p)^{1/p}}{\mathbb{E}(X)}$ for positive p-integrable random variable X. For $p = 2$, we have the usual *coefficient of variation* $\mathsf{CV}(X) = \mathsf{CV}_2(X) =$

$\sqrt{\mathbb{E}(X^2)}/\mathbb{E}(X)$. If $X \preceq_{cx} Y$, then $\mathsf{CV}_2(X) \leq \mathsf{CV}_2(Y)$ (in fact $\mathsf{CV}_p(X) \leq \mathsf{CV}_p(Y)$ for all $p \geq 1$).

2.4 Increasing convex order and convex order for random vectors

We shall need to compare not only random variables but random vectors as in [4, p.98] and [5, p.323]. For this, we can no longer appeal to repartition functions. Let $X = (X_1, \ldots, X_n)$ and $Y = (Y_1, \ldots, Y_n)$ be random vectors with finite mean.

We say that X *is less than* Y *in increasing convex order*, written $X \preceq_{icx} Y$, if and only if $\mathbb{E}(\varphi(X_1, \ldots, X_n)) \leq \mathbb{E}(\varphi(Y_1, \ldots, Y_n))$ for any increasing convex function $\varphi : \mathbb{R}^n \to \mathbb{R}$.

We say that X *is less than* Y *in convex order*, written $X \preceq_{cx} Y$, if and only if $\mathbb{E}(\varphi(X_1, \ldots, X_n)) \leq \mathbb{E}(\varphi(Y_1, \ldots, Y_n))$ for any convex function $\varphi : \mathbb{R}^n \to \mathbb{R}$. In this case, X and Y have the same mean.

Consider X following Normal distribution $\mathcal{N}(\mu, \Sigma)$ and X' following $\mathcal{N}(\mu', \Sigma')$. Then, $X \preceq_{cx} X'$ if and only if $\mu = \mu'$ and $\Sigma' - \Sigma$ is non-negative definite. The situation is not as clear cut for the *icx* order. If $\mu_X \geq \mu_Y$ and $\Sigma_X - \Sigma_Y > 0$ (non-negative definite), then $X \succeq_{icx} Y$. If $X \succeq_{icx} Y$, then $\mu_X \geq \mu_Y$ and $a^T(\Sigma_X - \Sigma_Y)a \geq 0$ for all vector $a \geq 0$ [4, p.100].

3 Generic results on environmental noise variability in population dynamics matrix models

In what follows, we shall consider a population described at discrete times $t = 0, \ldots, T$ (where T is the *horizon*), either by a scalar $n(t) \in \mathbb{R}$ or by a vector $n(t) = \big(n_1(t), \ldots, n_n(t)\big) \in \mathbb{R}^n$ which may be abundances at ages or stages. The *population size* is $N = \|n\| = n_1 + \cdots + n_n$.

The dynamical evolution of the population is supposed to be linear in the sense that

$$n(t+1) = A\big(\varepsilon(t)\big)n(t) \ , \quad t = 0, \ldots, T-1 \ , \tag{1}$$

where the matrix A is independent of $n(t)$ (no density-dependence effect, this is why we label such model of linear). On the other hand, the components A_{ij} of the matrix A may depend on the *environmental factors*, a vector $\varepsilon(t) = \big(\varepsilon_1(t), \ldots, \varepsilon_p(t)\big) \in \mathbb{R}^p$ at time t.

For instance, the components of the matrix A may depend linearly on the environmental factors, as in the expression

$$A\big(\varepsilon\big) = \begin{pmatrix} \overline{A}_{11} + \varepsilon_{11} & \cdots & \overline{A}_{1n} + \varepsilon_{1n} \\ \cdots & \cdots & \cdots \\ \overline{A}_{n1} + \varepsilon_{n1} & \cdots & \overline{A}_{nn} + \varepsilon_{nn} \end{pmatrix} \tag{2}$$

or may depend exponentially as in

$$A\big(\varepsilon\big) = \begin{pmatrix} \exp\big(\overline{A}_{11} + \varepsilon_{11}\big) & \cdots & \exp\big(\overline{A}_{1n} + \varepsilon_{1n}\big) \\ \cdots & \cdots & \cdots \\ \exp\big(\overline{A}_{n1} + \varepsilon_{n1}\big) & \cdots & \exp\big(\overline{A}_{nn} + \varepsilon_{nn}\big) \end{pmatrix} \ . \tag{3}$$

In this latter case, the components of the matrix A are log-convex function of the environmental factors. Recall that f is a log-convex function if $f > 0$ and $\log f$ is convex. Otherwise stated, f is the exponential of a convex function (as a consequence, a log-convex function is also convex).

In [6], different non linear models are recalled. When $\alpha = 0$, they are matrix models without density-dependency. Model (2a) exhibits components which are exponential in the environmental factor, while they are linear in models (2c) and (2d). Calculation shows that model (2b) has matrix components which are log-convex functions of the environmental factor.

We shall coin *environmental scenario* a temporal sequence $\varepsilon(\cdot) = \big(\varepsilon(0), \dots, \varepsilon(T-1)\big)$ of environmental factors.

Proposition 1 *Consider two environmental scenarii, one being more variable in increasing convex order than the other:* $\big(\varepsilon^M(0), \dots, \varepsilon^M(T-1)\big) \succeq_{icx} \big(\varepsilon^L(0), \dots, \varepsilon^L(T-1)\big)$. *Denote by* $N^M(T) = \|A\big(\varepsilon^M(T-1)\big) \cdots A\big(\varepsilon^M(0)\big)n(0)\|$ *and* $N^L(T) = \|A\big(\varepsilon^L(T-1)\big) \cdots A\big(\varepsilon^L(0)\big)n(0)\|$ *the corresponding populations sizes.*

Assume that the components $A_{ij}(\varepsilon_1, \dots, \varepsilon_p)$ *of the matrix* A *in* (1) *are nonnegative combinations of log-convex functions of the environmental factor* $(\varepsilon_1, \dots, \varepsilon_p)$. *Then, the more variable the scenario, the more variable the population size in the sense that*

$$N^M(T) \succeq_{icx} N^L(T) \;\; \textit{and} \;\; \log N^M(T) \succeq_{icx} \log N^L(T) \; . \tag{4}$$

As a consequence, $\mathbb{E}\left(N^M(T)\right) \geq \mathbb{E}\left(N^L(T)\right)$ *and* $\mathbb{E}\left(\log N^M(T)\right) \geq \mathbb{E}\left(\log N^L(T)\right)$.

In a sense, *environmental variability increases both mean population size and mean log-population size and makes them more variable.*

Proof. The components of the vector $n(T) = A\big(\varepsilon(T-1)\big) \cdots A\big(\varepsilon(0)\big)n(0)$ are sums of products of nonnegative combinations of log-convex functions of the environmental scenario. Therefore, by a property of log-convex functions [7], the components of the vector $n(T)$ are also log-convex functions of the environmental scenario, and so is the population size. Thus, the logarithm $\log N(T)$ of the population size is convex in $\big(\varepsilon(0), \dots, \varepsilon(T-1)\big)$. For any increasing convex function $\varphi : \mathbb{R} \to \mathbb{R}$, $\varphi\big(\log N(T)\big)$ is convex in $\big(\varepsilon(0), \dots, \varepsilon(T-1)\big)$ since convexity is preserved by left-composition with an increasing convex function. We end up by using the definition of increasing convex order for random vectors in §2.4: $\mathbb{E}\big[\varphi\big(\log N^M(T)\big)\big] \geq \mathbb{E}\big[\varphi\big(\log N^L(T)\big)\big]$. This precisely means that $\log N^M(T) \succeq_{icx} \log N^L(T)$.

Since a log-convex function is also convex, the population size $n(T)$ is a sum of convex functions of the environmental scenario. Then, the proof follows as above.

At last, we use the property that $X \succeq_{icx} Y \Rightarrow \mathbb{E}(X) \geq \mathbb{E}(Y)$ to compare the means.

□

Instead of total population, the result would still hold true with any positive weighted combination $a_1 n_1 + \cdots + a_k n_k$ where $a_i \geq 0$, or with $\log(a_1 n_1 + \cdots + a_k n_k)$ where $a_i \geq 0$,

As an illustration, consider the following scalar dynamic equation for population size $n(t+1) = \exp\big(r + \varepsilon(t)\big)n(t)$, for which we have $n(T) = \exp\big(rT + \varepsilon(0) + \cdots + \varepsilon(T-1)\big)n(0)$.

Hence, both $n(T)$ and $\log n(T)$ are convex functions of the environmental scenario $\varepsilon(\cdot) = (\varepsilon(0), \ldots, \varepsilon(T-1))$, so that environmental variability increases mean population size as may be seen in Figure 2. Indeed, the mean population size generated by a more variable environment is above the one by a less variable environment, for all times.

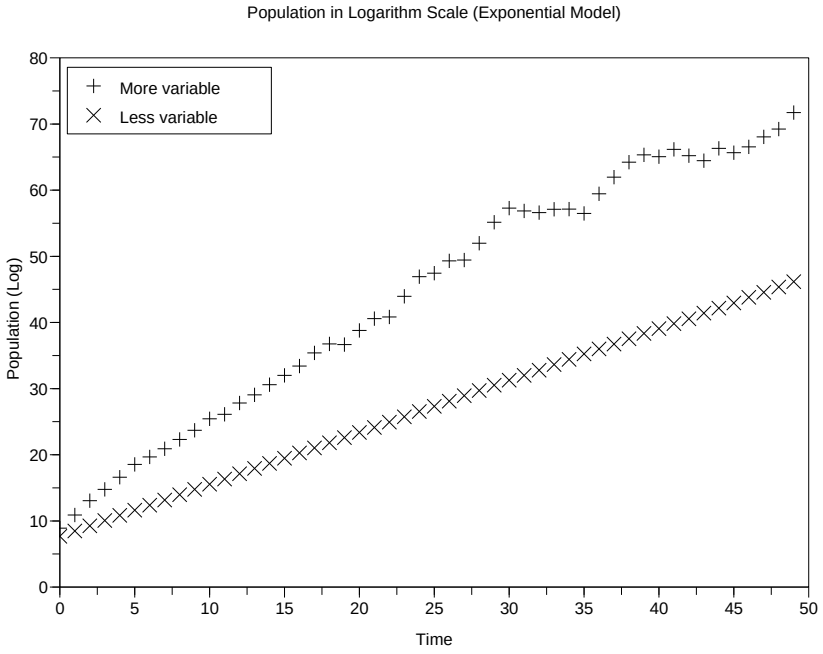


Figure 2: Environmental variability increases mean population size for a population model where growth rate depends exponentialy on environmental factor

4 Conclusion

We have used another notion of variability than the widely used variance or coefficient of variation, namely the so-called convex orders. We think that such partial orders may be of interest in theoretical ecology beyond this specific application.

To compare our approach with the literature, notice that, though we consider matrix population models, we make no ergodic assumption on the stochastic process A_0, A_1, ... However, we make separate assumptions, on the one hand on the environmental factors $\varepsilon(0), \ldots, \varepsilon(t)$ and, on the other hand, on the functional dependence $A_t = A\big(\varepsilon(t)\big)$.

With this approach, we obtain generic results which are not asymptotic in time, but valid at any time t and for a large class of functional dependence on the uncertainties.

Though the approach is different, our conclusions are consistent with the cases presented in Sect. 2. We extend the observation of Lande that, when adding environmental noise to growth rate on the log scale, environmental stochasticity increases the mean multiplicative

growth rate to matrix models. As to Tuljapurkar's asympotic approximation, we arrive at a different conclusion because his assumptions correspond to a matrix A depending linearly on the environmental factors as in (2), and our result does not cover this case.

Our general conclusion is, therefore, that the analytical dependence on environmental factors cannot be overlooked when trying to tackle the influence of variability. However, as shown in this paper, specific analytical dependence coupled with appropriate notion of variability lead to wide generic results, valid for all times and not only asymptotically, and requiring no assumptions of stationarity, of normality, of independency, etc.

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